

Shape of the Piriform Aperture in *Gorilla gorilla*, *Pan troglodytes*, and Modern *Homo sapiens*: Characterization and Polymorphism Analysis

MATTHIEU SCHMITTBUHL,¹ JEAN-MARIE LE MINOR,^{2*}
BERNARD ALLENBACH,³ AND ANDRÉ SCHAAF³

¹Federation of Odontological Research, INSERM U424, F-67085
Strasbourg, France

²Institute of Normal Anatomy, Faculty of Medicine,
F-67085 Strasbourg, France

³Institute of Geology, Louis Pasteur University, F-67084 Strasbourg, France

KEY WORDS piriform aperture; face; hominoids; Fourier analysis

ABSTRACT By using new methodologies based on automatic image analysis, the shape of the piriform aperture was analyzed in *Gorilla gorilla* (33 males, 13 females), *Pan troglodytes* (35 males, 22 females), and modern *Homo sapiens* (30 males, 12 females). The determination of the piriform aperture index (breadth/height) allowed the authors to demonstrate a marked elongation of the aperture in *Homo* compared with *Gorilla* and *Pan*. Individual characterization of the shape was possible with great precision and without ambiguity by using Fourier analysis. An absolute, interspecific partition between *Gorilla*, *Pan*, and *Homo* resulted from the canonical discriminant analysis of the Fourier descriptors. However, a closeness of shape between some individuals in *Pan* and some in *Gorilla* and *Homo* was observed, demonstrating a morphological continuum of the shape of the piriform aperture in hominoids: *Pan* was in intermediate position between *Gorilla* and *Homo*. Interspecific differences between *Homo* and the group *Pan-Gorilla* were explained principally by the differences in elongation (amplitude of the second harmonic) and pentagonality (amplitude of the fifth harmonic) and by differences in orientation of quadrangularity (phase of the fourth harmonic). Differences in the shape of the piriform aperture between *Pan* and *Gorilla* were explained by differences in orientation of elongation (phase of the second harmonic) and by differences in the component of triangularity (amplitude of the third harmonic). In *Gorilla* and *Pan*, the little, elongated, and relatively trapezoidal piriform aperture seems to be a shared primitive feature (plesiomorphic), whereas an elongated piriform aperture seems to be a characteristic and derived feature (apomorphic) of modern *Homo sapiens*. *Am J Phys Anthropol* 106:297-310, 1998. © 1998 Wiley-Liss, Inc.

The shape of the piriform aperture seems to be an informative morphologic characteristic of the hominoid face. A precise characterization of this shape in extant and well-identified species can be helpful for the proper interpretation and classification of extinct and fossil individuals. Most of the descriptions of this shape in anatomical and anthropological treatises are qualitative, and

the piriform aperture is characterized by such adjectives as piriform (Hershkovitz, 1977; Williams, 1995), pear-shaped (Macalister, 1898), cordiform (Poirier, 1896), quadrate (Macalister, 1898), square-rectangular,

*Correspondence to: Dr. J.-M. Le Minor, Institut d'Anatomie Normale, Faculté de Médecine, F-67085 Strasbourg, France.

Received 6 August 1997; accepted 12 April 1998.

or ovate (Hershkovitz, 1977). Quantitative data about the shape of the piriform aperture remain rare.

By using new methodologies based on automatic image analysis, the purpose of this work is to provide quantitative data on the shape of the piriform aperture and to allow an individual characterization for a better understanding of the interspecific relationships between *Gorilla gorilla*, *Pan troglodytes*, and modern *Homo sapiens*. The results will also demonstrate the utility of Fourier analysis to the objective study of irregular shapes.

MATERIALS AND METHODS

Osteological material

The skulls of 145 adult hominoid primates were examined in this study: 46 *Gorilla gorilla* (33 males, 13 females), 57 *Pan troglodytes* (35 males, 22 females), and 42 modern *Homo sapiens* (30 males, 12 females). All of the skulls showed complete eruption of the permanent dentition and could therefore be considered as adult subjects. They were free from pathological changes. These specimens came from the Institut d'Anatomie Normale (Faculté de Médecine, Strasbourg, France), the Institut et Musée de Zoologie (Université Louis Pasteur, Strasbourg), and the Laboratoire d'Anatomie Comparée (Muséum National d'Histoire Naturelle, Paris).

Image-analysis procedure

Image processing was performed with a microcomputer HP VL2[®] 486 DX2-66 MHz (Hewlett-Packard, Corvallis, OR) equipped with a frame grabber (Matrox Vision Processor). Image capture was performed with a CCD camera (I2S-NC 562BC). The camera was fixed on a macrophotographic stand. The visualization and the analysis of images were made with a software package (Visilog) providing all classical image-processing tools. The spatial resolution of image was 512×512 pixels. The Fourier analysis program used in this study was developed in Visual C++ language by Schmittbuhl et al. (1995).

Each skull was placed under the camera with the palatal plane parallel to the focal

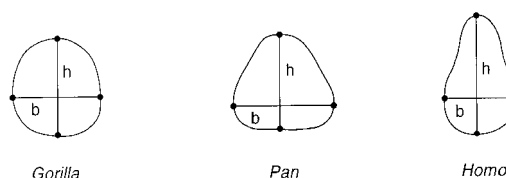


Fig. 1. Determination of the breadth (b) and height (h) of the piriform aperture in *Gorilla*, *Pan*, and *Homo*. The piriform aperture index corresponds to the ratio of the breadth of the piriform aperture to its height.

axis of the camera; this axis was also located in the median sagittal plane of the skull. The piriform aperture was extracted automatically by a binary threshold, transforming the gray-level image into a binary image. Then, the outline of the piriform aperture was extracted by a thinning operation. To eliminate size dependence, the area of the piriform aperture was scaled to a standard area.

Linear measurements and piriform aperture index

For each piriform aperture extracted, the *breadth of the piriform aperture* (maximum breadth of the piriform aperture) and the *height of the piriform aperture* (vertical distance between the lowest point and the highest point of the piriform aperture) were determined automatically. The *piriform aperture index*, corresponding to the ratio of the breadth of the piriform aperture to its height, was then calculated for each individual (Fig. 1).

Fourier analysis

To perform the Fourier analysis of the piriform aperture, it was necessary to express its outline in polar coordinates. The centroid (baricenter) of the outline of the piriform aperture was calculated. This centroid was used as the reference center for computing polar coordinates. The outline of the piriform aperture was then described by a discrete function $R(\theta)$, representing the length of a line joining a point of the outline to the centroid, θ being the angle made by this line with the horizontal axis. Polar coordinates of the whole outline were calculated at 128 equiangular intervals.

The outline represented by the discrete function $R(\theta)$ was then described by a Fourier series with the following mathematical expression:

$$R(\theta) = C_0 + \sum_{j=1}^n [C_j \cos(j\theta + \phi_j)].$$

In this expression, the components $C_0 - C_n$ and $\phi_0 - \phi_n$ are the *Fourier descriptors*, and correspond respectively to the amplitude and to the phase of each harmonic. C_j and ϕ_j defined one harmonic with the frequency j . The amplitude, C_j , represents the relative importance of the contribution of the j th harmonic to the whole shape, and the phase ϕ_j represents the angular orientation of the first lobe of the j th harmonic (Christopher and Waters, 1974; Flook, 1987; Lestrel et al., 1989; Schmittbuhl et al., 1995). Mathematically, the total number of harmonics that can be calculated is limited to half the number of sampled points of the outline (Press et al., 1992); in the present study, the Fourier descriptors were calculated in this manner for the first 64 harmonics (128 equiangular intervals/2).

For each harmonic, each individual was represented on a polar plot by a point defined by a module corresponding to the amplitude C_j and an argument corresponding to the phase ϕ_j . The representation of a sample of individuals corresponds to a scatter of points for each harmonic. A mean vector of each scatter of points is then computed, as developed by Schmittbuhl et al. (1995).

The inverse procedure of the expansion in Fourier series allowed the step-by-step reconstruction of the outline of each piriform aperture using an increasing number of harmonics. The different reconstructed outlines were compared visually with the original piriform aperture outline.

Statistical analysis

The statistical analysis was performed by using the SSPS statistical package (SAS Institute, Cary, NC). For each species, summary statistics of the piriform aperture index and of the Fourier descriptors (mean, \bar{X} ; standard deviation, S.D.; coefficient of variation, C.V. = S.D./ \bar{X}) were performed. The quality of fit with the normal distribution was estimated by using the Kolmogorov-

TABLE 1. Piriform aperture index in Gorilla gorilla, Pan troglodytes, and Homo sapiens: Summary statistics

Species	No.	Piriform aperture index ¹		
		\bar{X}	S.D.	C.V.
Gorilla M	33	1.02	0.10	0.10
Gorilla F	13	1.08	0.12	0.11
Pan M	35	1.10	0.14	0.13
Pan F	22	1.16	0.10	0.09
Homo M	30	0.72	0.07	0.10
Homo F	12	0.77	0.05	0.06

¹ \bar{X} , mean; S.D., standard deviation; C.V., coefficient of variation; M, males; F, females.

Smirnov test (Nie et al., 1975). Pairwise, between-group comparisons of the piriform aperture index and of the Fourier descriptors were then performed by Wilcoxon tests (Johnson and Bhattacharyya, 1996) to examine the intraspecific and interspecific differences. For each harmonic, nonparametric Kruskal-Wallis tests (Nie et al., 1975) were used to detect amplitudes and phases for which significant between-group differences were observed.

A multivariate statistical approach using canonical discriminant analysis was run on the pairs of Fourier descriptors. The first pair of Fourier descriptors (C_0 , ϕ_0) was excluded from the statistical analysis, because C_0 was a constant resulting from the normalization of the areas, and because ϕ_0 was always equal to zero. For each individual, the result of the canonical discriminant analysis was represented on a two-dimensional plot that was defined by the first and the second canonical discriminant axes (Reyment et al., 1984). The correlations of each Fourier descriptor with each canonical discriminant function were calculated. For the three species studied, the representation of the set of individuals corresponds to a scatter of points. The centroid of each scatter was determined, and the distances between each individual and the three centroids were calculated. Each individual was then allocated to the species with the closest centroid. The numbers of correctly classified individuals were then calculated.

RESULTS

Summary statistics of the piriform aperture index are listed in Table 1. The results of intraspecific and interspecific compari-

TABLE 2. Piriform aperture index: Comparisons between *Gorilla gorilla*, *Pan troglodytes*, and *Homo sapiens* (Wilcoxon test)¹

Species	<i>Gorilla</i> F	<i>Pan</i> M	<i>Pan</i> F	<i>Homo</i> M	<i>Homo</i> F
<i>Gorilla</i> M	$P < 0.05$	$P < 0.01$	$P < 0.001$	$P < 0.001$	$P < 0.001$
<i>Gorilla</i> F	—	n.s.	n.s.	$P < 0.001$	$P < 0.001$
<i>Pan</i> M		—	n.s.	$P < 0.001$	$P < 0.001$
<i>Pan</i> F			—	$P < 0.001$	$P < 0.001$
<i>Homo</i> M				—	n.s.
<i>Homo</i> F					—

¹ n.s. Indicates a significance level greater than 0.05. M, males; F, females.

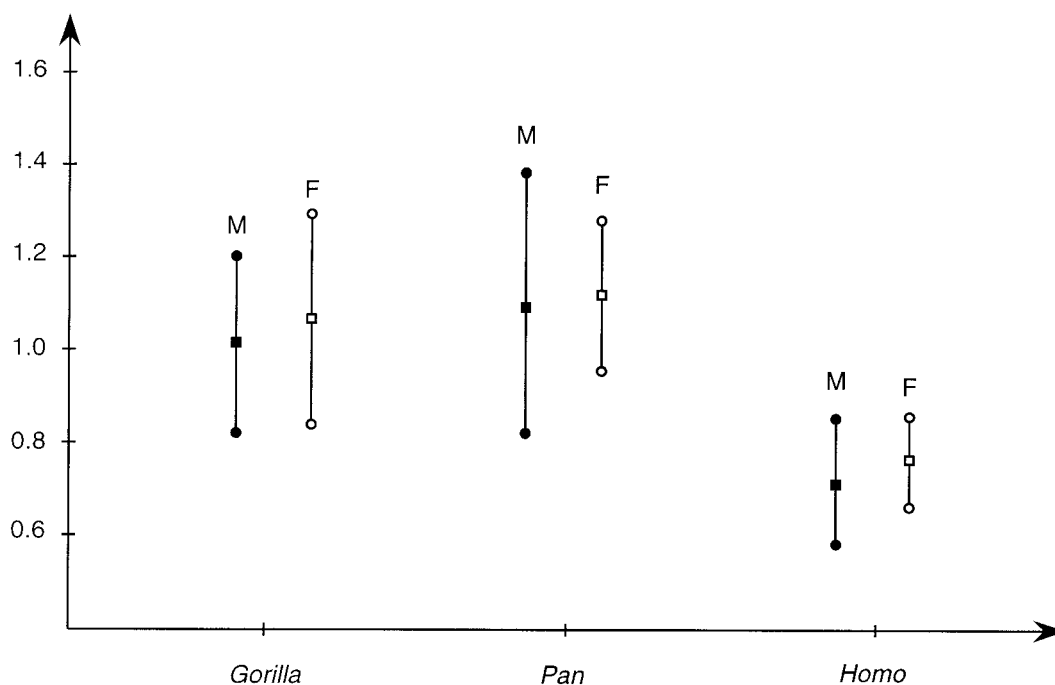


Fig. 2. Piriform aperture index. Results in the 46 *Gorilla* (33 males, 13 females), 57 *Pan* (35 males, 22 females), and 42 *Homo* (30 males, 12 females) studied. M, males; F, females; square, mean; circle, ± 2 standard deviations.

sons of this piriform aperture index are given in Table 2 and illustrated in Figure 2.

Summary statistics of the Fourier descriptors of the piriform aperture in *Gorilla*, *Pan*, and *Homo* are given in Tables 3 and 4. Because no differences in the Fourier descriptors were observed after the 13th harmonic, only the first 13 pairs of descriptors were retained in the tables and in the statistical analysis. No differences were demonstrated in the Fourier descriptors between males and females in the same species; therefore, the males and females from the same species were combined, and the tables report only a single result for each species.

The results of the interspecific comparison of the Fourier descriptors are listed in Tables 5 and 6. The polar representations of the Fourier descriptors (Fig. 3), the comparative representation of the mean vectors of the three species (Fig. 4), the step-by-step reconstructions (Fig. 5), and the geometrical contributions of the Fourier harmonics (Fig. 6) are illustrated only for the first six Fourier harmonics.

Polymorphism analysis

Individual characterization of the shape of the piriform aperture was possible with great precision and without ambiguity by

TABLE 3. *Fourier analysis of the outline of the piriform aperture in Gorilla gorilla, Pan troglodytes, and Homo sapiens: Summary statistics of Fourier amplitudes¹*

Fourier amplitudes	Gorilla			Pan			Homo		
	\bar{X}	S.D.	C.V.	\bar{X}	S.D.	C.V.	\bar{X}	S.D.	C.V.
C ₁	0.98	0.70	0.71	1.11	0.55	0.50	3.67	0.96	0.26
C ₂	4.11	2.58	0.63	4.72	2.87	0.61	14.88	3.22	0.22
C ₃	4.15	1.81	0.44	7.83	2.09	0.27	7.41	1.45	0.20
C ₄	2.07	0.94	0.45	1.44	0.69	0.48	2.07	1.04	0.50
C ₅	0.90	0.69	0.77	1.00	0.54	0.54	2.91	0.79	0.27
C ₆	0.65	0.41	0.63	0.74	0.45	0.61	0.83	0.47	0.57
C ₇	0.50	0.29	0.58	0.59	0.32	0.54	0.76	0.31	0.41
C ₈	0.38	0.19	0.50	0.37	0.20	0.54	0.43	0.25	0.58
C ₉	0.29	0.16	0.55	0.28	0.15	0.54	0.29	0.17	0.59
C ₁₀	0.22	0.12	0.55	0.25	0.14	0.36	0.26	0.11	0.42
C ₁₁	0.18	0.10	0.56	0.19	0.10	0.53	0.20	0.11	0.55
C ₁₂	0.17	0.09	0.53	0.17	0.08	0.47	0.17	0.09	0.53
C ₁₃	0.11	0.08	0.73	0.15	0.08	0.53	0.17	0.08	0.47

¹ Males and females are combined. \bar{X} , mean; S.D., standard deviation; C.V., coefficient of variation.TABLE 4. *Fourier analysis of the outline of the piriform aperture in Gorilla gorilla, Pan troglodytes, and Homo sapiens: Summary statistics of Fourier phases¹*

Fourier phases	Gorilla			Pan			Homo		
	\bar{X}	S.D.	C.V.	\bar{X}	S.D.	C.V.	\bar{X}	S.D.	C.V.
ϕ_1	119.12	77.02	0.65	132.11	75.05	0.57	90.56	13.45	0.15
ϕ_2	97.94	45.50	0.46	181.42	45.70	0.25	89.15	5.04	0.06
ϕ_3	30.50	5.31	0.17	29.27	3.32	0.11	28.60	4.35	0.15
ϕ_4	44.11	9.08	0.21	43.57	16.49	0.38	90.48	13.50	0.15
ϕ_5	38.16	17.88	0.47	31.37	19.26	0.61	52.95	3.96	0.07
ϕ_6	60.21	9.05	0.15	25.98	12.46	0.48	29.22	12.82	0.44
ϕ_7	32.98	11.32	0.34	32.17	9.04	0.28	15.30	12.50	0.82
ϕ_8	20.35	12.80	0.63	23.33	11.28	0.48	25.93	14.97	0.58
ϕ_9	17.91	11.99	0.67	18.59	10.24	0.55	24.54	10.10	0.41
ϕ_{10}	16.55	10.24	0.62	20.79	12.01	0.58	18.96	9.96	0.53
ϕ_{11}	14.72	9.20	0.63	18.46	9.26	0.50	19.32	8.29	0.43
ϕ_{12}	14.86	8.94	0.60	14.16	9.08	0.64	14.17	8.29	0.59
ϕ_{13}	13.99	8.59	0.61	13.21	7.42	0.56	13.22	8.69	0.66

¹ Males and females are combined. \bar{X} , mean; S.D., standard deviation; C.V., coefficient of variation.TABLE 5. *Comparison of Fourier amplitudes in Gorilla gorilla, Pan troglodytes, and Homo sapiens (Wilcoxon test)¹*

Fourier amplitudes	Pan-Gorilla	Pan-Homo	Gorilla-Homo
C ₁	n.s.	$P < 0.01$	$P < 0.01$
C ₂	n.s.	$P < 0.01$	$P < 0.01$
C ₃	$P < 0.01$	n.s.	$P < 0.01$
C ₄	$P < 0.01$	$P < 0.01$	n.s.
C ₅	n.s.	$P < 0.01$	$P < 0.01$
C ₆	n.s.	n.s.	n.s.
C ₇	n.s.	$P < 0.05$	$P < 0.01$
C ₈	n.s.	n.s.	n.s.
C ₉	n.s.	n.s.	n.s.
C ₁₀	n.s.	n.s.	n.s.
C ₁₁	n.s.	n.s.	n.s.
C ₁₂	n.s.	n.s.	n.s.
C ₁₃	$P < 0.05$	n.s.	$P < 0.05$

¹ Males and females are combined. n.s. Indicates a significance level greater than 0.05.TABLE 6. *Comparison of Fourier phases in Gorilla gorilla, Pan troglodytes, and Homo sapiens (Wilcoxon test)¹*

Fourier phases	Pan-Gorilla	Pan-Homo	Gorilla-Homo
ϕ_1	n.s.	$P < 0.01$	$P < 0.01$
ϕ_2	$P < 0.01$	$P < 0.01$	n.s.
ϕ_3	n.s.	n.s.	n.s.
ϕ_4	n.s.	$P < 0.01$	$P < 0.01$
ϕ_5	n.s.	$P < 0.01$	$P < 0.01$
ϕ_6	$P < 0.01$	n.s.	$P < 0.01$
ϕ_7	n.s.	$P < 0.01$	$P < 0.01$
ϕ_8	n.s.	n.s.	n.s.
ϕ_9	n.s.	$P < 0.05$	$P < 0.01$
ϕ_{10}	n.s.	n.s.	n.s.
ϕ_{11}	$P < 0.05$	n.s.	n.s.
ϕ_{12}	n.s.	n.s.	n.s.
ϕ_{13}	n.s.	n.s.	n.s.

¹ Males and females are combined. n.s. Indicates a significance level greater than 0.05.

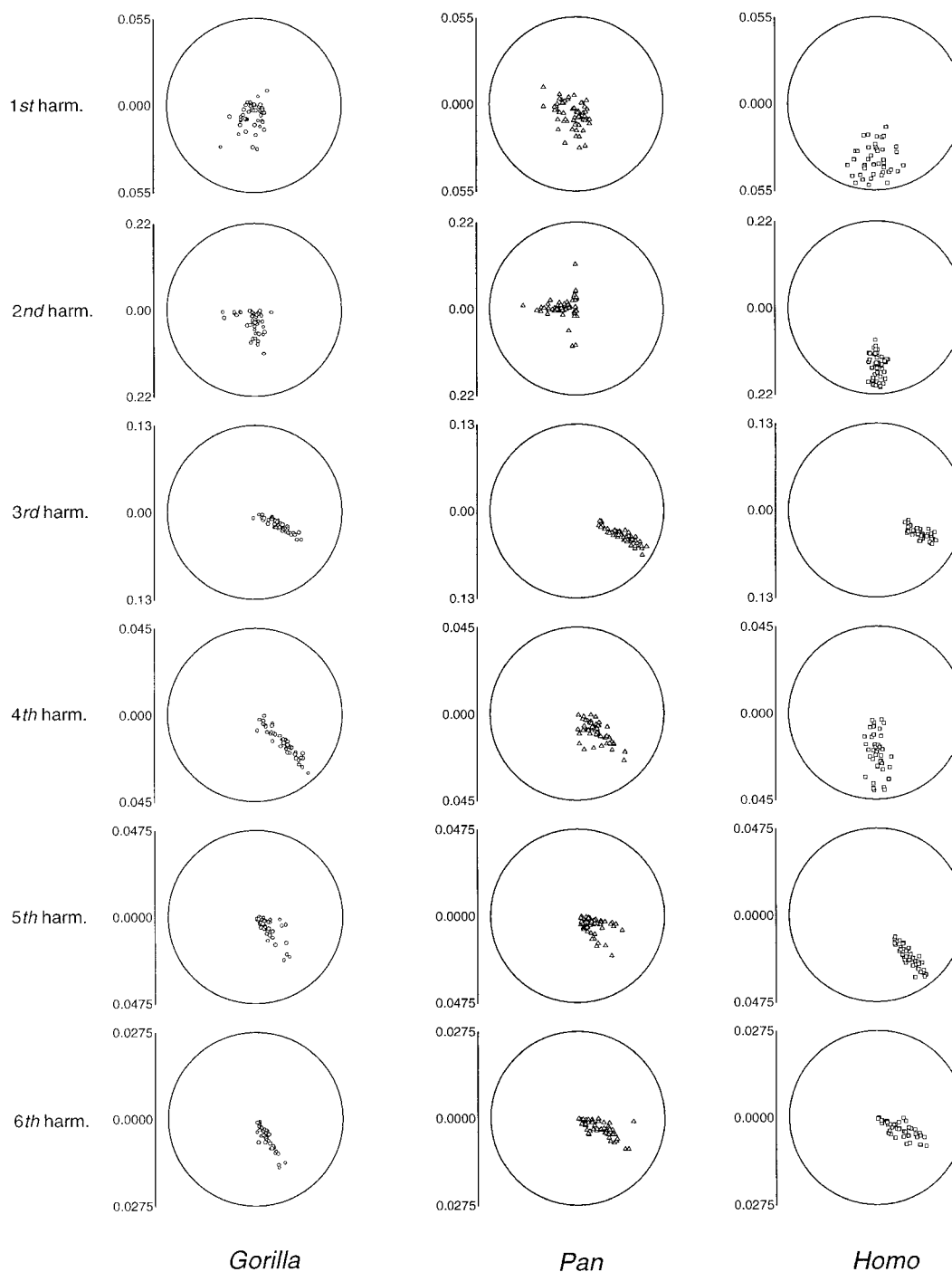


Fig. 3. Fourier descriptors of the piriform outline in *Gorilla*, *Pan*, and *Homo* (polar representations of the six first harmonics; harm.). Each individual was represented in polar coordinates by a point defined by a module corresponding to the amplitude and an argument corresponding to the phase of the harmonic considered. Amplitude scale is indicated for each polar representation.

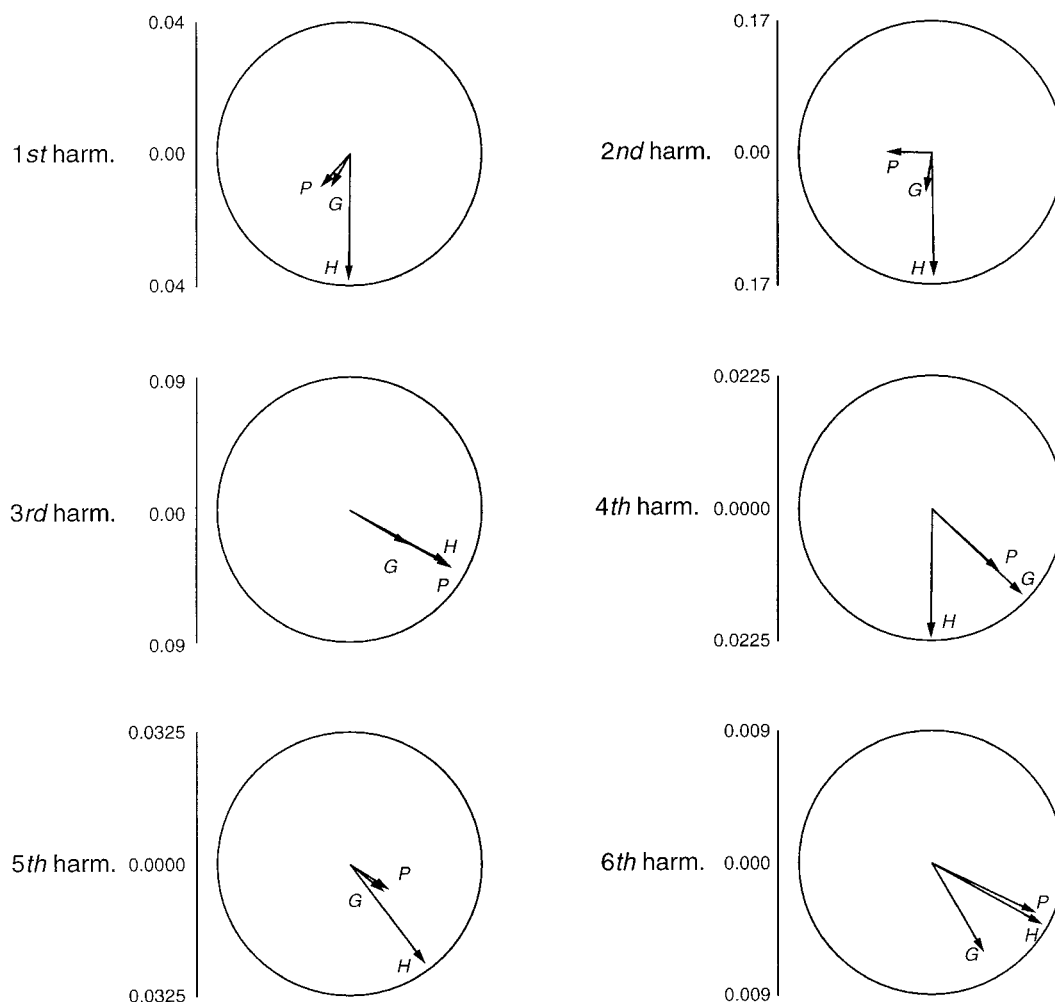


Fig. 4. Comparative polar representations of the mean vectors of the six first harmonics (harm.; Fourier descriptors) of the piriform outline in *Gorilla* (G), *Pan* (P), and *Homo* (H). Amplitude scale is indicated for each polar representation.

using Fourier analysis. A polymorphism of the piriform shape was demonstrated for the three hominoid species studied (Figs. 3, 7). The individuals in *Gorilla* and *Pan* presented a morphology of the piriform aperture that was more variable than that in *Homo*, as demonstrated by the important values of the coefficient of variation of the first harmonics (1–6) in *Gorilla* and *Pan* compared with those of *Homo* (Tables 3 and 4).

Morphological similarities of the piriform aperture existed between some individuals of *Gorilla* and *Pan* and between some indi-

viduals of *Pan* and *Homo* (Figs. 7 and 8); on the other hand, no individual in *Gorilla* and *Homo* presented similar shapes (Figs. 7 and 8). *Pan* presented multiple morphological intermediates, among which some were close to *Gorilla*, and others were close to *Homo* (Figs. 7 and 8).

The clouds of individuals of each species presented no overlapping, as demonstrated by the canonical discriminant analysis for *Gorilla*, *Pan*, and *Homo* of the first 13 pairs of Fourier descriptors (Fig. 7). A first canonical discriminant function accounted for 64.66% of the total variance, whereas a

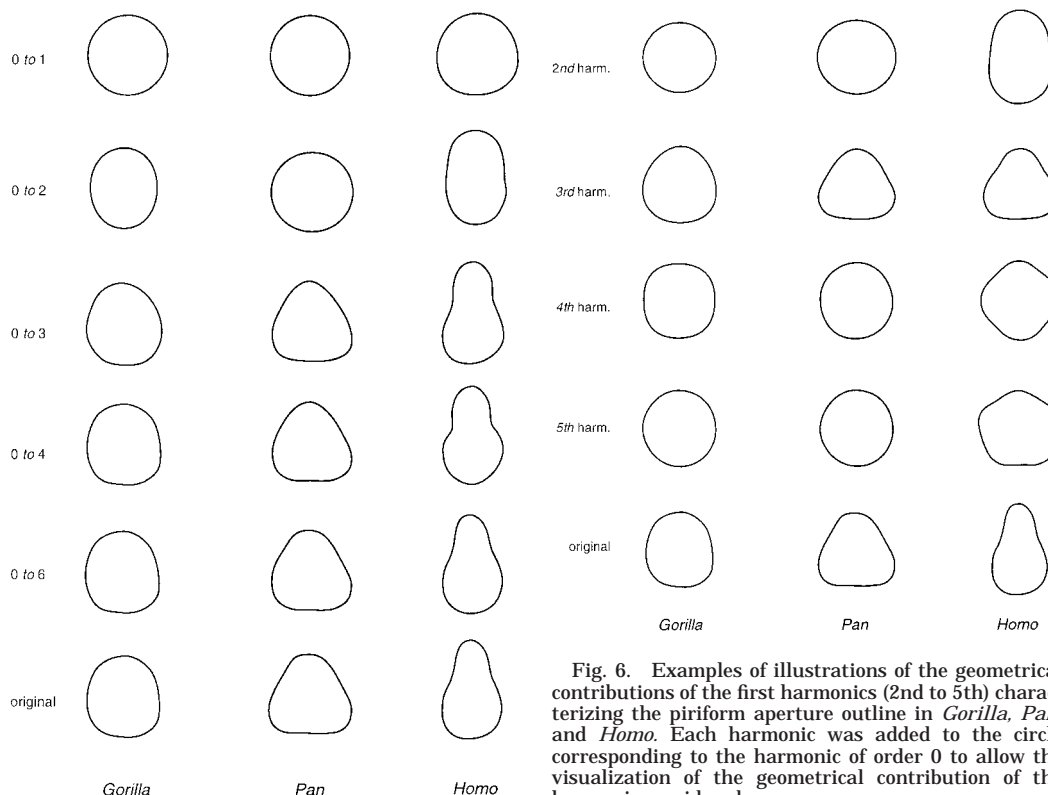


Fig. 5. Examples of step-by-step reconstructions of the piriform outline in *Gorilla*, *Pan*, and *Homo* (males) with an increasing number of harmonics. The piriform outline was validly reconstructed by using the six first harmonics.

second canonical discriminant function explained the remaining 35.44%. The first canonical discriminant function differentiated *Homo* from the group *Gorilla-Pan*, and the second canonical discriminant function separated *Gorilla* from *Pan*. Allocation of each individual to the species with the closest centroid allowed the correct classification of all individuals. The interspecific differences corresponded mainly to amplitude and phase differences in the first six harmonics. The first canonical discriminant function (Can1) was correlated principally with C_1 , C_2 , ϕ_4 , and C_5 , and the second canonical discriminant function (Can2) was correlated with ϕ_2 , C_3 , and ϕ_6 (Table 7).

Shape characterization

A smooth aspect characterized the shape of the piriform aperture in *Gorilla*, *Pan*, and

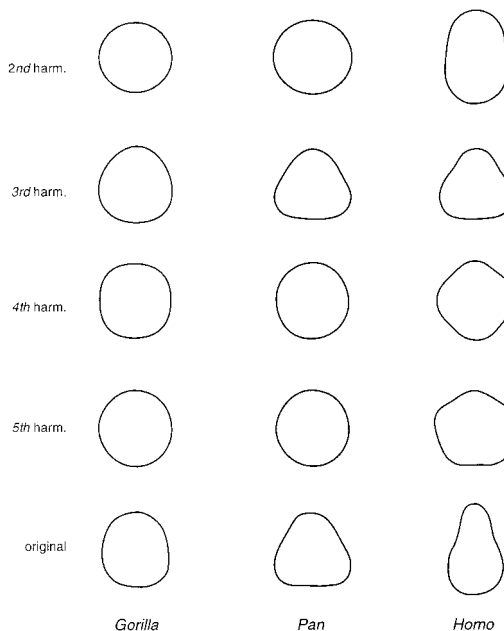


Fig. 6. Examples of illustrations of the geometrical contributions of the first harmonics (2nd to 5th) characterizing the piriform aperture outline in *Gorilla*, *Pan*, and *Homo*. Each harmonic was added to the circle corresponding to the harmonic of order 0 to allow the visualization of the geometrical contribution of the harmonic considered.

Homo. This morphological characteristic was demonstrated by the fact that the greatest amplitudes of the Fourier harmonics (1–6) and by the fact that the mean amplitude values of each species decreased as the order of the harmonics increased (Table 3). This was also confirmed by the quality of the reconstructions of the piriform outline with the use of the first six harmonics (Fig. 5).

A relative elongation of the piriform aperture, corresponding to a relative elliptical shape, was particularly marked in *Homo* compared with that observed in *Gorilla* and *Pan*, as demonstrated by the importance of the amplitude of the second harmonic in *Homo* ($C_2 = 14.88$) compared with that observed in *Gorilla* and *Pan* (respectively, $C_2 = 4.11$ and $C_2 = 4.72$). Moreover, this elliptical shape was a dominant morphological feature in *Homo*, because the amplitude of the second harmonic in *Homo* was far greater than all other harmonic amplitudes (Table 3). The mean orientation of the long

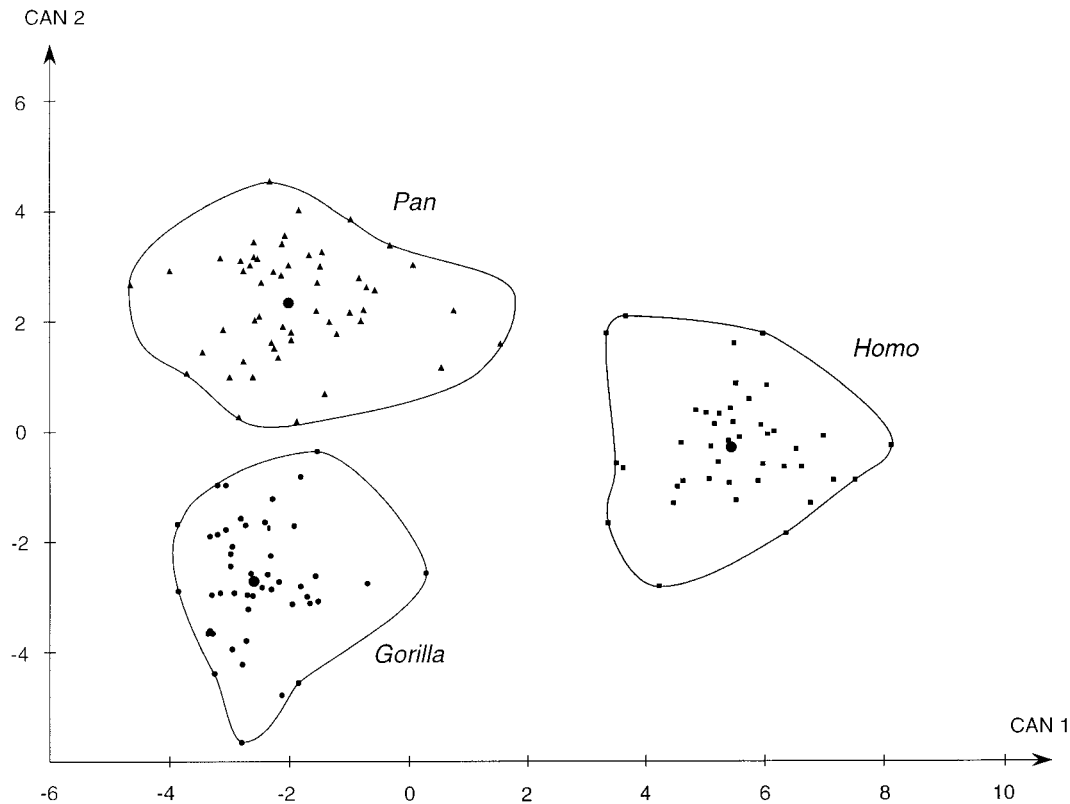


Fig. 7. Results of the canonical discriminant analysis of the 13 first pairs of Fourier descriptors for the 145 individuals studied: 46 *Gorilla* (circles), 57 *Pan* (triangles), and 42 *Homo* (squares). Two-dimensional plot defined by the first and second canonical discriminant axes (CAN).

axis of the corresponding ellipse (phase of the second harmonic ϕ_2) was vertical in *Homo* and *Gorilla* and horizontal in *Pan* (Table 4, Figs. 4, 6). This relative elongation was also demonstrated by the piriform aperture index. This index was the most important in *Pan*, was reduced in *Homo*, and was intermediate in *Gorilla*. The females in *Gorilla* were characterized by an index close to that of *Pan*; in *Pan* and *Homo*, no significant difference was found between this index in males and females of each species. The piriform aperture index was less than 1 (vertical elongation) in 42 of 42 individuals studied in *Homo* (100.0%), in 14 of 46 individuals in *Gorilla* (30.4%), and in 8 of 57 individuals in *Pan* (14.0%; Table 8).

The piriform aperture was relatively triangular in the three hominoid species, as demonstrated by the relative importance of the amplitude of the third harmonic compared

with the amplitudes of the other harmonics (Table 3). The triangularity appeared to be more marked in *Pan* and *Homo* (respectively, $C_3 = 7.83$ and $C_3 = 7.41$) compared with *Gorilla* ($C_3 = 4.15$). Triangularity seemed to be a dominant morphological feature in *Pan*, because the amplitude of the third harmonic in *Pan* was greater than all of the other harmonic amplitudes of this species (Table 3). The mean orientation of the triangular shape was nearly the same for the three hominoid species, as indicated by the phase angular values of the third harmonic (*Gorilla*, $\phi_3 = 30.50^\circ$; *Pan*, $\phi_3 = 29.27^\circ$; *Homo*, $\phi_3 = 28.60^\circ$; Fig. 4). Geometrically, the triangular shape presented an inferior horizontal base in the three hominoid species (Fig. 6).

A relative quadrangularity of the piriform aperture was observed principally in *Gorilla* and *Homo* and seemed to be less

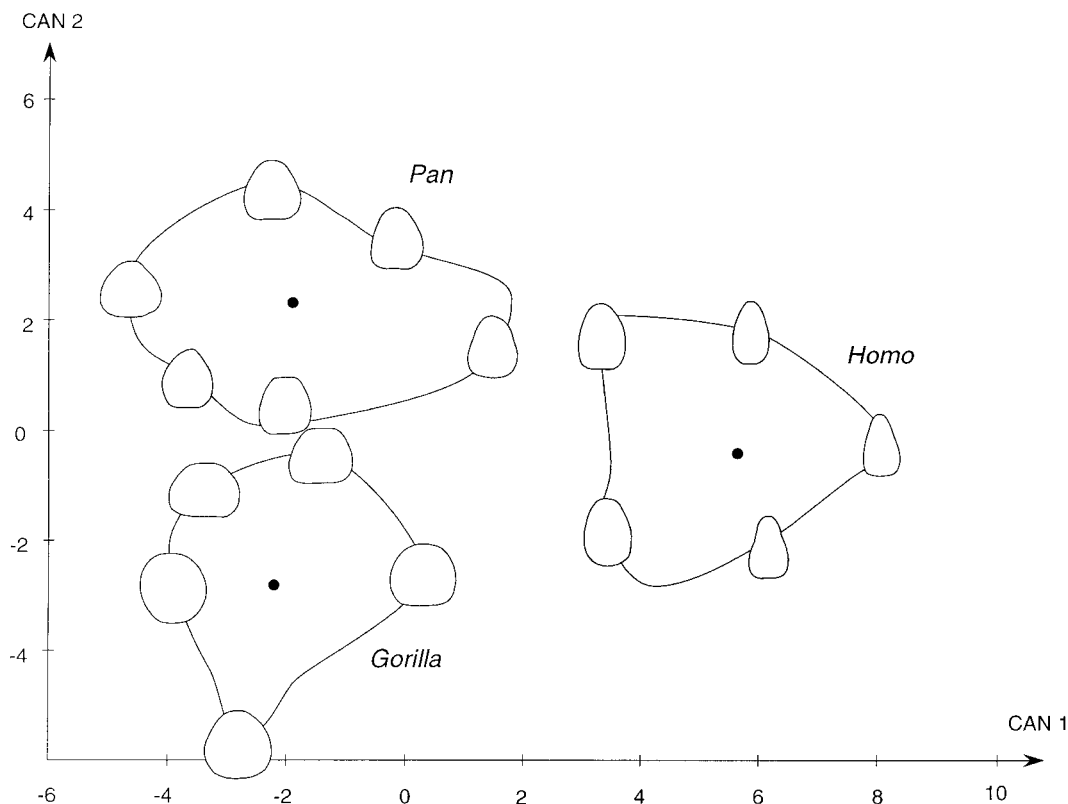


Fig. 8. Illustration of the variability of the shape of the piriform aperture outline in *Gorilla*, *Pan*, and *Homo*. The canonical discriminant analysis of the 13 first pairs of Fourier descriptors represent, for each species, the individuals that were the farthest from the centroid of the cloud. A closeness of shape between some individuals in *Pan* and some in *Gorilla* and *Homo* was observed, demonstrating a morphological continuum of the shape of the piriform aperture in hominoids.

marked in *Pan* (Fig. 6), as demonstrated by the relative importance of the amplitude of the fourth harmonic in *Gorilla* and *Homo* (respectively, $C_4 = 2.07$ and $C_4 = 2.07$) compared with that in *Pan* ($C_4 = 1.44$). Quadrangularity in the three hominoid species was always less marked than elongation and triangularity, as indicated by the reduced amplitude of the fourth harmonic in the three species compared with that of the second harmonic and that of the third harmonic (Table 3). The orientation of the squared shape was close in *Gorilla* and *Pan*, whereas that observed in *Homo* was significantly different, as indicated by the phase of the fourth harmonic (*Gorilla*, $\phi_4 = 44.11^\circ$; *Pan*, $\phi_4 = 43.57^\circ$; *Homo*, $\phi_4 = 90.48^\circ$; Fig. 4). Geometrically, the squared shape in *Gorilla* and *Pan* presented an oblique diagonal

(45°) and, in *Homo*, a vertical diagonal (90° ; Fig. 6).

The pentagonality of the piriform aperture, quantified by the amplitude of the fifth harmonic, was more marked in *Homo* than in *Gorilla* and *Pan* (Figs. 4, 6), as indicated by the relative importance of the amplitude of the fifth harmonic in *Homo* ($C_5 = 2.91$) compared with that observed in *Gorilla* and *Pan* (respectively, $C_5 = 0.90$ and $C_5 = 1.00$). Moreover, the pentagonality in *Homo* prevailed slightly over quadrangularity, because the amplitude of the fifth harmonic was a little higher than that of the fourth harmonic; inversely, pentagonality in *Gorilla* and *Pan* was less marked than quadrangularity (Table 3). The orientation of the pentagonal shape in *Homo* was significantly different from that of *Gorilla* and that of

TABLE 7. Canonical discriminant analysis of Fourier descriptors in *Gorilla gorilla*, *Pan troglodytes*, and *Homo sapiens*: Correlations of Fourier descriptors with each canonical discriminant function¹

First canonical discriminant function				Second canonical discriminant function			
Fourier amplitudes	<i>r</i>	Fourier phases	<i>r</i>	Fourier amplitudes	<i>r</i>	Fourier phases	<i>r</i>
C ₁	0.48 ²	φ ₁	-0.07	C ₁	-0.03	φ ₁	0.04
C ₂	0.50 ²	φ ₂	-0.16	C ₂	-0.04	φ ₂	0.40 ²
C ₃	0.12	φ ₃	-0.02	C ₃	0.33 ²	φ ₃	-0.02
C ₄	0.04	φ ₄	0.47 ²	C ₄	-0.13	φ ₄	-0.07
C ₅	0.40 ²	φ ₅	0.15	C ₅	-0.03	φ ₅	-0.09
C ₆	0.04	φ ₆	-0.18	C ₆	0.03	φ ₆	-0.29 ²
C ₇	0.09	φ ₇	-0.22 ²	C ₇	0.03	φ ₇	0.01
C ₈	0.04	φ ₈	0.04	C ₈	-0.01	φ ₈	0.03
C ₉	0.01	φ ₉	0.08	C ₉	0.00	φ ₉	0.00
C ₁₀	0.03	φ ₁₀	0.01	C ₁₀	0.03	φ ₁₀	0.06
C ₁₁	0.01	φ ₁₁	0.04	C ₁₁	0.00	φ ₁₁	0.06
C ₁₂	-0.01	φ ₁₂	-0.01	C ₁₂	-0.01	φ ₁₂	-0.01
C ₁₃	0.06	φ ₁₃	0.00	C ₁₃	0.07	φ ₁₃	-0.01

¹ Males and females are combined. *r*, Coefficient of correlation.² Greatest correlation coefficients (*r* ≥ 0.20).TABLE 8. Qualitative characteristics of the shape of the piriform aperture in *Gorilla gorilla*, *Pan troglodytes*, and *Homo sapiens* resulting from the piriform index and the Fourier analysis¹

Species	Elongation			Triangularity		Quadrangularity		Pentagonality	
	Amplitude	Ellipse orientation ³	Index of elongation ³	Amplitude	Triangle orientation	Amplitude	Square orientation	Amplitude	Pentagon orientation
<i>Gorilla</i>	++ ²	Horizontal (15.2) Vertical (30.4) Oblique (54.4)	Horizontal (69.6) Vertical (30.4)	++	Inferior horizontal base	+	Oblique diagonal (≈45°)	0	—
<i>Pan</i>	++	Horizontal (45.6) Vertical (19.3) Oblique (35.1)	Horizontal (85.0) Vertical (14.0)	+++	Inferior horizontal base	+	Oblique diagonal (≈45°)	0	—
<i>Homo</i>	++++	Vertical (100.0)	Vertical (100.0)	+++	Inferior horizontal base	+	Vertical diagonal (≈90°)	++	Inferior horizontal base

¹ Males and females are combined.² The number of crosses is proportional to the amplitude of the geometrical characteristic considered (0 to ++++).³ Values within brackets correspond to the proportion of individuals in each species presenting a given orientation.

Pan, as demonstrated by the phase angular values of the fifth harmonic (*Gorilla*, φ₅ = 38.16°; *Pan*, φ₅ = 31.37°; *Homo*, φ₅ = 52.95°; Fig. 4). Geometrically, the pentagonal shape in *Homo* presented an inferior horizontal base (Fig. 6).

The contributions of the harmonics of higher order (more than six) were relatively reduced, as indicated by their relatively small amplitude values compared with those of the first six harmonics (Table 3). The small contribution of these harmonics indicated that they were of little geometrical interest. The major morphologic characteristics of the shape of the piriform aperture in *Gorilla*, *Pan*, and *Homo* resulting from the determination of the piriform aperture index and the Fourier analysis are summarized quantitatively in Table 8.

DISCUSSION

Methodological aspects

The shape of the piriform aperture has been described quantitatively by some authors by using the anthropological nasal index, which corresponds to the ratio of the maximum nasal breadth to the maximum nasal length, the length and the breadth, respectively, are measured on skulls as the distance from the nasal spine to the nasofrontal suture and as the widest distance between the left and right piriform crests (Martin and Saller, 1956; Russel, 1956; Glanville, 1969). By using this index, human skulls were classified into leptorrhinians (index between 42 and 47), mesorrhinians (index between 48 to 52), platyrrhinians (index from 53 to 58), and hyperplatyrrhin-

ians (index greater than 58; Russel, 1956). In the present study, the index determined corresponds strictly to parameters of piriform aperture; thus, the results are not comparable with those from the literature. However, the indices used take into account only a very small part of the shape information.

Fourier analysis has been applied previously with success to a wide variety of irregular shapes that are difficult to analyze with conventional approaches (Erich and Weinberg, 1970; Christopher and Waters, 1974; Johnson et al., 1985, 1988, 1992; Jacobshagen, 1986; Lestrel and Roche, 1986; Flook, 1987; O'Higgins and Williams, 1987; Le Minor et al., 1989; Lestrel et al., 1989; O'Higgins and Johnson, 1993; Schmittbuhl et al., 1995). The use of Fourier analysis is justified, because this methodology takes into account all of the information of an outline. In the present study, we used the Fourier descriptors, in contrast to most previous Fourier analysis based on the determination of the Fourier coefficients. This allows the direct representation of the geometrical contribution of the Fourier harmonics, which would not have been possible directly with the Fourier coefficients (Lestrel et al., 1989; Schmittbuhl et al., 1995). This geometric interpretation allows quantification of the more or less marked elongation, triangularity, quadrangularity, and pentagonality of the shape of the piriform aperture. The resulting quantitative data presented in this study are entirely original and cannot be compared with previous data from the literature.

The same projection plane, perpendicular to the palatal plane, was used for image analysis of all piriform apertures. Indeed, to compare the shape in a series of particular structures, all of their outlines must be studied in the same reference plane. Orientation of the skull in the palatal plane is justified by its easy reproducibility and by its relative parallelism to the mean axis of the nasal cavities in hominoids. However, the use of other classical planes of reference (e.g., orbitomeatal plane, vestibular plane) also would have lead to similar results.

Shape of the piriform aperture in hominoids

The only sexual dimorphism that was demonstrated concerned the piriform aperture index in *Gorilla*, the females in *Gorilla* being close to *Pan*. No sexual dimorphism in the shape of the piriform aperture was demonstrated with the Fourier analysis in *Gorilla*, *Pan*, or *Homo*. This result, at first sight, is paradoxical, because sexual dimorphism is well described in *Gorilla* and *Pan* (Diebarch, 1986; Schmid and Stratil, 1986; Uytterschaut, 1986; O'Higgins et al., 1990; O'Higgins and Dryden, 1993; Schmittbuhl et al., 1996). This may be explained easily by the fact that sexual dimorphism affects principally the size, and not the shape, of the piriform aperture, the size being normalized in the Fourier analysis in order to characterize only the shape.

An intraspecific variability in the shape of the piriform aperture exists in *Gorilla*, *Pan*, and *Homo* and seems more marked in *Gorilla* and *Pan* than in *Homo* (Tables 3 and 4, Fig. 7). The variability of the direction of the piriform elongation is particularly marked in *Gorilla* and *Pan*, in which the elongation could be either horizontal (69.6% of individuals in *Gorilla*, 86.0% in *Pan*) or vertical (30.4% in *Gorilla*, 14.0% in *Pan*); on the other hand, it is always vertical in *Homo* (100.0%; Table 8). This constant vertical elongation in *Homo*, compared with the variability observed in *Gorilla* and *Pan*, is also demonstrated by Fourier analysis (phase of the second Fourier harmonic; Table 8).

Absolute interspecific partition between *Gorilla*, *Pan*, and *Homo* resulted from the canonical discriminant analysis of the Fourier descriptors, despite the variability observed in the three hominoid species studied. Interspecific differences between *Homo* and the group *Pan-Gorilla* are explained principally by the differences in elongation (amplitude of the second harmonic) and pentagonality (amplitude of the fifth harmonic) and by differences in orientation in quadrangularity (phase of the fourth harmonic; Tables 7 and 8, Fig. 6). Differences in shape of the piriform aperture between *Pan* and *Gorilla* are explained by differences in

orientation of elongation (phase of the second harmonic) and by differences in the component of triangularity (amplitude of the third harmonic; Tables 7 and 8, Fig. 6).

A closeness of shape between some individuals in *Pan* and some individuals in *Gorilla* and *Homo* is observed, despite the absolute partition between the three hominoid species (Figs. 7, 8). The existence of a morphological continuum of the shape of the piriform aperture in hominoids, thus, is demonstrated by Fourier analysis. *Pan* is in an intermediate position between *Gorilla* and *Homo* (Figs. 7, 8), and this is in agreement with most other morphologic and genetic studies (Andrews, 1986; Bishop and Friday, 1986; Martin, 1986).

The mean elongation of the piriform aperture presents a paradoxical relationship with facial elongation in the three hominoid species studied. *Gorilla* and *Pan* are characterized by an elongated face (Endo, 1973; Preuschoft et al., 1986; Schmittbuhl et al., 1996) and a short piriform aperture, whereas *Homo* presents a short face and an elongated aperture (Fig. 5).

Evolutionary perspectives

In fossil hominids, a preliminary visual analysis of facial representations (Rak, 1983, 1985; Klein, 1989; Aiello and Dean, 1990) using the results of the present study demonstrates that *Australopithecus*, *Homo habilis*, and *Homo erectus* present a little elongated and relatively trapezoidal piriform aperture, close to those quantified by Fourier analysis in *Pan* and *Gorilla*. The early *Homo sapiens* (Klein, 1989) are characterized by an intermediate piriform elongation. The elongation seems to be the greatest in modern *Homo sapiens*. A relatively elongated piriform aperture, thus, seems to be a characteristic and derived feature (apomorphic) in *Homo*, whereas the nasal shape in *Gorilla* and *Pan* seems to be a shared primitive feature (plesiomorphic). The application of the present methodology to extinct and fossil individuals can provide new quantitative data that could allow the classification of individuals whose systematic position remains obscure.

LITERATURE CITED

- Aiello L, and Dean C (1990) An Introduction to Human Evolutionary Anatomy. London: Academic Press.
- Andrews P (1986) Molecular evidence for catarrhine evolution. In B Wood, L Martin, and P Andrews (eds.): Major Topics in Primate and Human Evolution. Cambridge: Cambridge University Press, pp. 107–129.
- Bishop MJ, and Friday AE (1986) Molecular phylogeny. In B Wood, L Martin, and P Andrews (eds.): Major Topics in Primate and Human Evolution. Cambridge: Cambridge University Press, pp. 151–156.
- Christopher RA, and Waters JA (1974) Fourier analysis as a quantitative descriptor of miospore shape. *J. Paleontol.* 48:697–709.
- Dierbach A (1986) Interspecific variability and sexual dimorphism in the skulls of *Pan troglodytes verus*. In M Pickford, and B Chiarelli (eds.): Sexual Dimorphism in Living and Fossil Primates. Firenze: Il Sedicesimo, pp. 41–50.
- Ehrlich R, and Weinberg B (1970) An exact method for the characterization of grain shape. *J. Sediment. Petrol.* 40:205–212.
- Endo B (1973) Stress analysis of the gorilla face. *Primates* 14:37–45.
- Flook A (1987) The quantitative measurement of particle shape. *Acta Stereol.* 6:1009–1027.
- Glanville EV (1969) Nasal shape, prognathism and adaption in Man. *Am. J. Phys. Anthropol.* 30:29–38.
- Hershkovitz P (1977) Living New World Monkeys (Platyrrhini), Vol 1. Chicago: University of Chicago Press.
- Jacobshagen B (1986) Size and shape of the orbital outline: A multivariate comparison and analysis of intraspecific variation in four hominoid species. In JG Else, and PC Lee (eds.): Primate Evolution. Cambridge: University Press, pp. 281–288.
- Johnson DR, O'Higgins P, and McAndrew TJ (1985) Measurement of biological shape: A general method applied to mouse vertebra. *J. Embryol. Exp. Morphol.* 90:363–377.
- Johnson DR, O'Higgins P, and McAndrew TJ (1988) The relationship between age, size and shape in upper thoracic vertebrae of the mouse. *J. Anat.* 161:73–82.
- Johnson DR, O'Higgins P, McAndrew TJ, and Kida MY (1992) The inheritance of vertebral shape in the mouse. I. A study using Fourier analysis to examine patterns of inheritance in the morphology of cervical and upper thoracic vertebrae. *J. Anat.* 180:507–514.
- Johnson RA, and Bhattacharyya GK (1996) Statistics. Principles and Methods, 3rd ed. New York: John Wiley and Sons.
- Klein RG (1989) The Human Career. Human Biological and Cultural Origins. Chicago: University of Chicago Press.
- Le Minor JM, Pister L, and Kahn E (1989) Shape description in osteology using automatic Fourier analysis. Example of the human atlas. *Arch. Anat. Histol. Embryol.* 72:69–79.
- Lestrel PE, and Roche AF (1986) Cranial base shape variation with age: A longitudinal study of shape using Fourier analysis. *Hum. Biol.* 58:527–540.
- Lestrel PE, Sarnat BG, and McNabb EG (1989) Carapace growth of the turtle *Chrysemys scripta*: A longitudinal study of shape using Fourier analysis. *Anat. Anz.* 168:135–143.
- Macalister A (1898) The apertura pyriformis. *J. Anat.* 32:223–230.
- Martin L (1986) Relationships among great apes and humans. In B Wood, L Martin, and P Andrews (eds.): Major Topics in Primate and Human Evolution. Cambridge: Cambridge University Press, pp. 161–187.

- Martin R, and Saller K (1956) *Lehrbuch der Anthropologie*, Vol 3. Stuttgart: Fischer.
- Nie NH, Hull JG, Jenkins JG, Steinberg K, and Bennet DH (1975) *Statistical package for the social sciences*. New York: McGraw-Hill.
- O'Higgins P, and Dryden IL (1993) Sexual dimorphism in hominoids: Further studies of craniofacial shape differences in *Pan*, *Gorilla*, and *Pongo*. *J. Hum. Evol.* 24:183–205.
- O'Higgins P, and Johnson DR (1993) The inheritance of vertebral shape in the mouse II. A study using Fourier analysis to examine the inheritance of patterns of vertebral variation in the cervical and upper thoracic vertebral column. *J. Anat.* 182:65–73.
- O'Higgins P, and Williams NW (1987) An investigation into the use of coefficients in characterizing cranial shape in primates. *J. Zool.* 211:409–430.
- O'Higgins P, Moore WJ, Johnson DR, and McAndrew TJ (1990) Patterns of cranial sexual dimorphism in certain groups of extant hominoids. *J. Zool.* 222:399–420.
- Poirier P (1896) *Traité d'Anatomie Humaine*, 2nd ed. T. 1. Paris: Masson.
- Press WH, Teukolsky SA, Vetterling WT, and Flannery SA (1992) *Numerical Recipes in C. The Art of Scientific Computing*, 2nd ed. Cambridge: Cambridge University Press.
- Preuschoft H, Demes B, Meyer M, and Bär HF (1986) The biomechanical principles realised in the upper jaw of long-snouted primates. In JG Else, and PC Lee (eds): *Primate Evolution*. Cambridge: Cambridge University Press, pp. 249–264.
- Rak Y (1983) *Australopithecine Face*. London: Academic Press.
- Rak Y (1985) Australopithecine taxonomy and phylogeny in light of facial morphology. *Am. J. Phys. Anthropol.* 66:281–287.
- Reyment RA, Blackitch RE, and Campbell NA (1984) *Multivariate Morphometrics*, 2nd ed. London: Academic Press.
- Russel IW (1956) The nasal index—Anthropological and clinical. *Am. J. Phys. Anthropol.* 65:171–199.
- Schmid P, and Stratil Z (1986) Growth changes, variations and sexual dimorphism of the gorilla skull. In JG Else, and PC Lee (eds.): *Primate Evolution*. Cambridge: Cambridge University Press, pp. 239–247.
- Schmittbuhl M, Allenbach B, Schaaf A, and Le Minor JM (1995) Description et classification de formes biologiques par les méthodes de Fourier. In A Wackenheim and G Zöllner (eds.): *Informatique et Imagerie Médicale*. Paris: Masson, pp. 85–99.
- Schmittbuhl M, Le Minor JM, and Schaaf A (1996) Relative position and extent of the nasal and orbital openings in *Gorilla*, *Pan*, and human species from the study of their areas and centres of area. *Folia Primatol.* 67:182–192.
- Uytterschaut HT (1986) Sexual dimorphism in human skulls. A comparison of sexual dimorphism in different populations. In M Pickford, and B Chiarelli (eds.): *Sexual Dimorphism in Living and Fossil Primates*. Firenze: Il Sedicesimo, pp. 113–120.
- Williams PL (1995) *Gray's Anatomy*, 38th ed. New York: Churchill Livingstone.